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Early to Middle Devonian Ceratoikiscidae (Radiolaria) from the Yokokurayama Group in the Kurosegawa Terrane, Southwest Japan

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Abstract. **This paper focuses on ceratoikiscid radiolarians from the Devonian Nakahata Formation of the Yokokurayama Group in the Kurosegawa Terrane. The fauna is assigned to the Emsian to Eifelian (late Early to early Middle Devonian). There are 13 species of radiolarians, including 4 new species, which belong to the genera *Ceratoikiscum*, *Glanta*, *Protoholoeciscus*, *Circulaforma* and *Helenifore*. The morphology and stratigraphic distribution of the genera suggest that *Protoholoeciscus* evolved from *Ceratoikiscum* via *Glanta* with the process of acquisition of shell.**

Key words : Ceratoikiscidae, Early to Middle Devonian, Kurosegawa Terrane, Radiolaria, Yokokurayama Group

Introduction

Ceratoikiscidae characterized by triangular skeletal framework is one of the guide taxa for Middle Paleozoic radiolarian biostratigraphy. In recent years, many species of Late Devonian Ceratoikiscidae have been described from various localities of the world and keen interest has been focused on setting up the Upper Devonian radiolarian zones (Cheng, 1986 ; Schwartzapfel and Holdsworth, 1996). From the Lower to Middle Devonian, reports of occurrences of Radiolaria have quite recently been accumulating (Wakamatsu *et al.*, 1990 ; Umeda, 1996, in press b ; Stratford and Aitchison, 1997). Four Lower to Middle Devonian radiolarian zones are proposed from the Kurosegawa Terrane (Umeda, in press a). However, paleontological research of Early to Middle Devonian Ceratoikiscidae is still insufficient.

Many species of Ceratoikiscidae, belonging to the genera *Ceratoikiscum, Glanta, Protoholoeciscus, Circulaforma* and *Helenifore*, were found from the Lower to Middle Devonian Nakahata Formation of the Yokokurayama Group in the Kurosegawa Terrane. The radiolarians are described and phylogenetic significances of these species are discussed in this paper.

Well-preserved radiolarians were obtained from some horizons of the sections examined in this study (Figures 5, 7, 8). The studied radiolarians are listed in Table 1. The collected rock samples were put into a bowl with 5% HF solution for 24 hours. The residues were gathered on a 200 mesh sieve. Radiolarians were picked with a very fine brush under a binocular microscope, and observed with a scanning electoron microscope. Type and figured specimens are registered and deposited in the Department of Geosciences, Osaka City University.

Geologic setting

The Kurosegawa Terrane of the Outer Zone of Southwest Japan is situated as a klippe upon the Jurassic accretionary complex of the Chichibu Belt (Figure 1-A). Paleozoic unmetamorphosed sedimentary strata are widely distributed in the Kurosegawa Terrane. Siluro-Devonian strata have been known from the Yokokurayama area (Figure 1-B) and were named as the Yokokurayama Group (Hirata, 1966).

The Yokokurayama Group is subdivided into six formations, namely the Gomi, Fukata, Ichiyama, Joryu, Nakahata and Ochi formations in ascending order (Umeda, 1998). The Nakahata Formation consists of acidic tuff, mudstone, tuffaceous sandstone and conglomerate. Rock samples for radiolarian research were collected from the acidic tuff and mudstone layers of Sections A, B and C in the Nakahata Formation (Figures 2, 3).

Estimated thickness of Section A is about 23 m. Section A consists of acidic tuff layers and tuffaceous sandstone layers (Figures 3, 4). The acidic tuff layers are composed of vitric tuff layers of 3 to 7 cm thickness, and are rhythmically interbedded with tuffaceous mudstone layers. Color of the tuff is green, dark green, gray and red. A single tuffaceous mudstone layer ranges from several millimeters to several

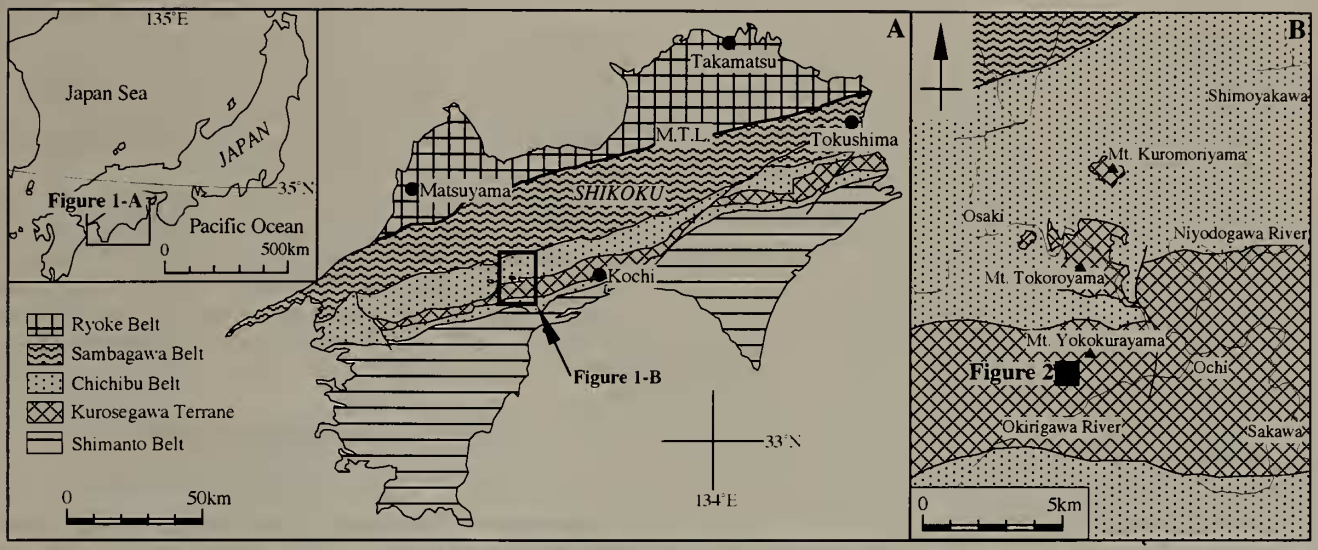


Figure 1. Index map showing the study area.

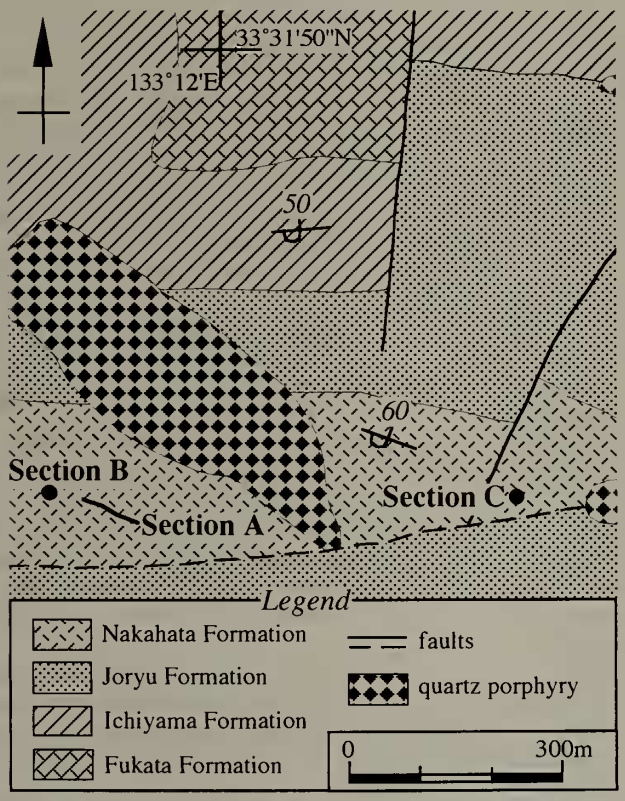


Figure 2. Geologic map and distribution of the examined sections.

centimeters thick and the color is white, yellow, light red and dark red. The tuffaceous sandstone is light green and fine- to medium-grained. Section B, about 4 m thick, is composed of dark red mudstone layers and green to red vitric tuff layers. Estimated thickness of Section C is about 6 m. Rocks of Section C consist of light green vitric acidic tuff layers and tuffaceous sandstone layers. A bed of the tuff is 5 to 20 cm in thickness. Parallel laminations are commonly observed in acidic tuff and tuffaceous sandstone layers. The acidic tuff and mudstone include many radiolarian remains and sponge spicules. The reddish vitric tuff comprises volcanic glasses in abundance.

Radiolarian zones and age

Four Early to Middle Devonian radiolarian zones, namely the *Futobari solidus, Trilonche* (?) sp. A, *Glanta fragilis* and *Protoholoeciscus hindea* zones in ascending order, have been proposed recently (Umeda, in press a). The lower part of Section A (2F to 3A) and the lower to middle part of Section B (37C and 37D) are assigned to the *G. fragilis* Zone. The upper part of Section A (3B to 3N) and the upper part of Section B (37E) are assigned to the *Pr. hindea* Zone. *Protoholoeciscus triangularis* (Wakamatsu, Sugiyama and Furutani) and *Glanta yokokurayamaensis* sp. nov. in Section C possess bladed rods, while the rods of *Glanta* and *Protoholoeciscus* in Sections A and B are circular in cross section. Bladed rods can be regarded as a rather evolved feature (Nazarov and Ormiston, 1985). This evidence suggests that Section C is situated at a higher stratigraphic level than the *Pr. hindea* Zone. The *G. fragilis* Zone is assigned to the Emsian to Eifelian (late Early Devonian–early Middle Devonian) and the *Pr. hindea* Zone to the Eifelian.

Systematic paleontology

Subclass Radiolaria Müller, 1858
Order Polycystina Ehrenberg, 1838, emend. Riedel, 1967
Suborder Albaillellaria Deflandre, 1953, emend. Holdsworth, 1969
Family Ceratoikiscidae Holdsworth, 1969
Genus ***Ceratoikiscum*** Deflandre, 1953

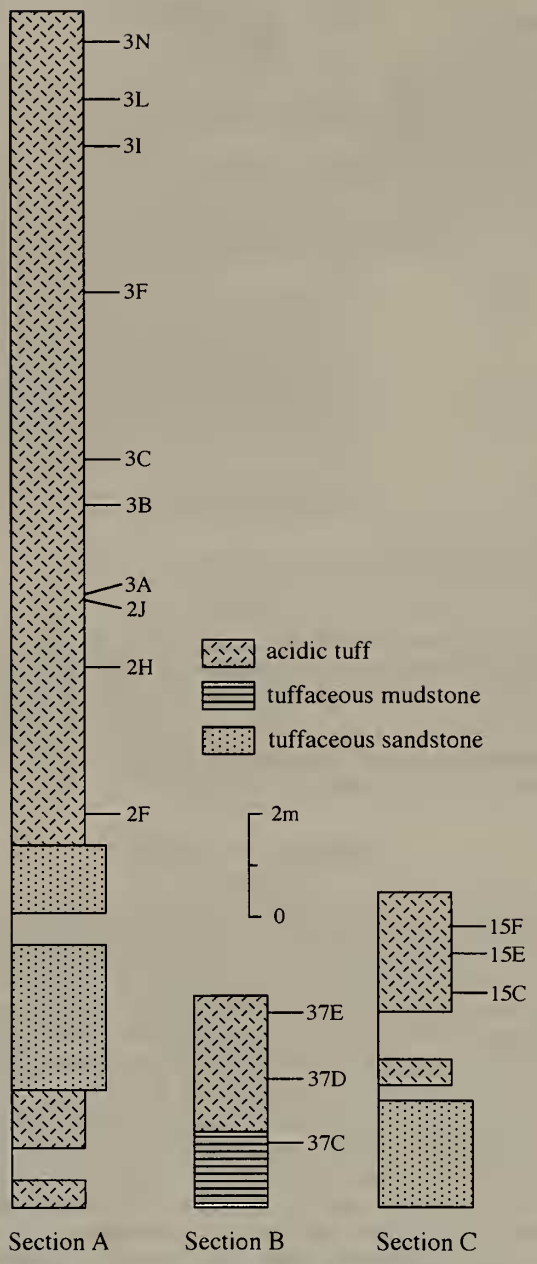


Figure 3. Columnar sections of the examined sections showing lithologic and sampling horizons.

Ceratoikiscum lyratum Ishiga, 1988

Figures 5-1—3

Ceratoikiscum lyratum Ishiga, 1988, p. 74, pl. 1, figs. 4-5; Ishiga, 1992, p. 392-395, fig. 9, 1-6; Aitchison, Hada, Ireland and Yoshikura, 1996, p.59, pl. 1-3, 4; 3-4, 5; Umeda, 1997, p. 21, pl. 1, figs, 15-18, pl. 3, figs, 10-13.

Ceratoikiscum vimineum Wakamatsu, Sugiyama and Furutani, 1990, p. 179-180, pl. 11, figs. 1-5; Furutani, 1996, fig. 7, 6.

Ceratoikiscum sp. Aitchison, Hada and Yoshikura, 1991, fig. 3, A-B.

Material.—Ten specimens from 2F, 3A, 3I, 3N in Section A, 37C and 37D in Section B and 15E in Section C.

Remarks.—This species possesses a developed patagium and long and slender extratriangular rods.

Range and occurrence.—Late Silurian to Middle Devonian time. The Upper Silurian and Lower Devonian in the Konomori area, central Kochi (Ishiga, 1988, 1992; Aitchison *et al*., 1991, 1996; Umeda, 1997) and the Nakahata Formation in the Yokokurayama area (Wakamatsu *et al*., 1990; Furutani, 1996), both in the Kurosegawa Terrane, Southwest Japan.

Ceratoikiscum turgidum sp. nov.

Figures 5-4, 5

Diagnosis.—This species is characterized by a well-developed lamellar patagium with a porous swell around the junction of a- and i-rods.

Description.—A distinctive swell is thick and spongy. Pores on the swell are circular to oval. Lamellar patagium is perforated and developed in horizontal plane. A.t., b.t. and i.t. (see Figure 6) rim the interior sides of the lamellar patagium. Central opening is subtriangular to suboval. Patagial tissue is weakly developed around the junction of b- and i-rods. A- and b-rods are curved and i-rod is much straighter. A.a. and b.d. are sturdy and long. B.v. and i.v. are short and rather conical. All rods are circular in cross section. Caveal ribs remain uncertain.

Measurements.—Measured features are shown in Figure 6-a.

Length of w.c.: 109-126, average 118, based on 4 specimens, in μm.

Material.—Four specimens from 37C in Section B and 15E in Section C.

Comparison.—This species differs from other species of *Ceratoikiscum* in having a thick swell around the junction of a- and i-rods. This species bears resemblance to *C. kochiense* Umeda in possessing developed lamellar patagium. This also is similar to *Glanta fragilis* Wakamatsu, Sugiyama and Furutani in having developed lamellar patagium, sturdy a.a., short b.v. and i.v., but it differs from *Glanta* in lacking a shell.

Range and occurrence.—Possible Emsian age (late Early Devonian time) to Eifelian age (early Middle Devonian time). Nakahata Formation of the Yokokurayama Group.

Etymology.—This name is derived from the Latin adjective *turgidus*, meaning inflated.

Type specimen.—Holotype OCU PR 0137 (Figure 5-4) from 37C.

Genus ***Glanta*** Wakamatsu, Sugiyama and Furutani, 1990; emend. herein

Type species.—*Glanta fragilis* Wakamatsu, Sugiyama and Furutani, 1990, p. 180-181, pl. 12.

Emended diagnosis.—Triangular skeletal framework with bilaterally symmetric porous shell which is situated between

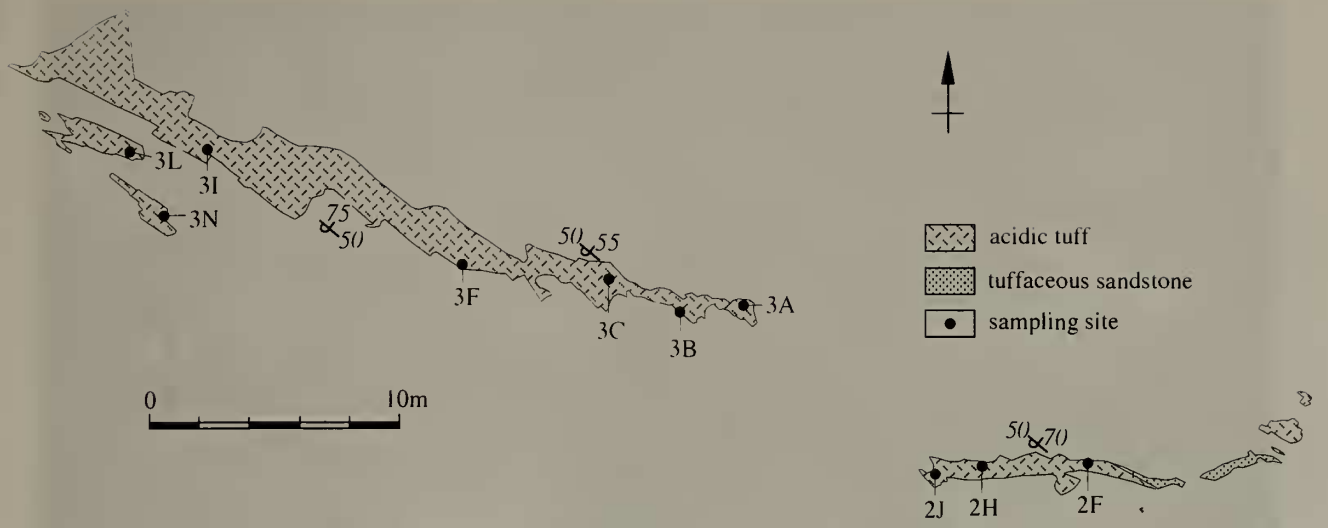


Figure 4. Route map of the Section A showing sampling sites.

Table 1. List of studied radiolarian fossils from the Nakahata Formation in the Yokokurayama Group.

	Section A										Section B			Section C		
RADIOLARIA \ SAMPLE NO.	2F	2H	2J	3A	3B	3C	3F	3I	3L	3N	37C	37DF	37E	15C	15E	15F
Ceratoikiscum lyratum Ishiga	+			+				+		+	+	+			+	
C. turgidum sp. nov.											+				+	
Glanta fragilis Wakamatsu, Furutani and Sugiyama	+	+	+	+							+	+	+			
G. sp.											+					
G. yokokurayamaensis sp. nov.														+	+	+
Circulaforma (?) sp. aff. *C.* sp. A														+	+	+
Helenifore sp. A Stratford and Aitchison								+	+	+				+	+	+
He. sp. B											+					
Protoholoeciscus sp.													+		+	
Pr. hindea Aitchison					+	+	+	+	+	+			+			
Pr. spinosus sp. nov.					+	+		+	+	+						
Pr. ochiensis sp. nov.														+	+	+
Pr. triangularis (Wakamatsu, Furutani and Sugiyama)														+	+	+

b.d. and i.d or i.t..

Remarks.—Wakamatsu *et al*. (1990) described the new genus *Glanta* which has a porous or lamellar shell. Central framework is triangular with five to six extratriangular rods. A.t. and the dorsal portion of i.t. are covered by the shell (Wakamatsu *et al*., 1990). Later, Aitchison (1993) separated a species with lamellar shell from *Glanta* as a new genus *Protoholoeciscus*. Stratford and Aitchison (1997) suggested that the species of *Glanta* described by Wakamatsu *et al*. (1990) might be best placed within *Protoholoeciscus*, which can be differentiated from *Glanta* on the basis of its having an imperforate shell.

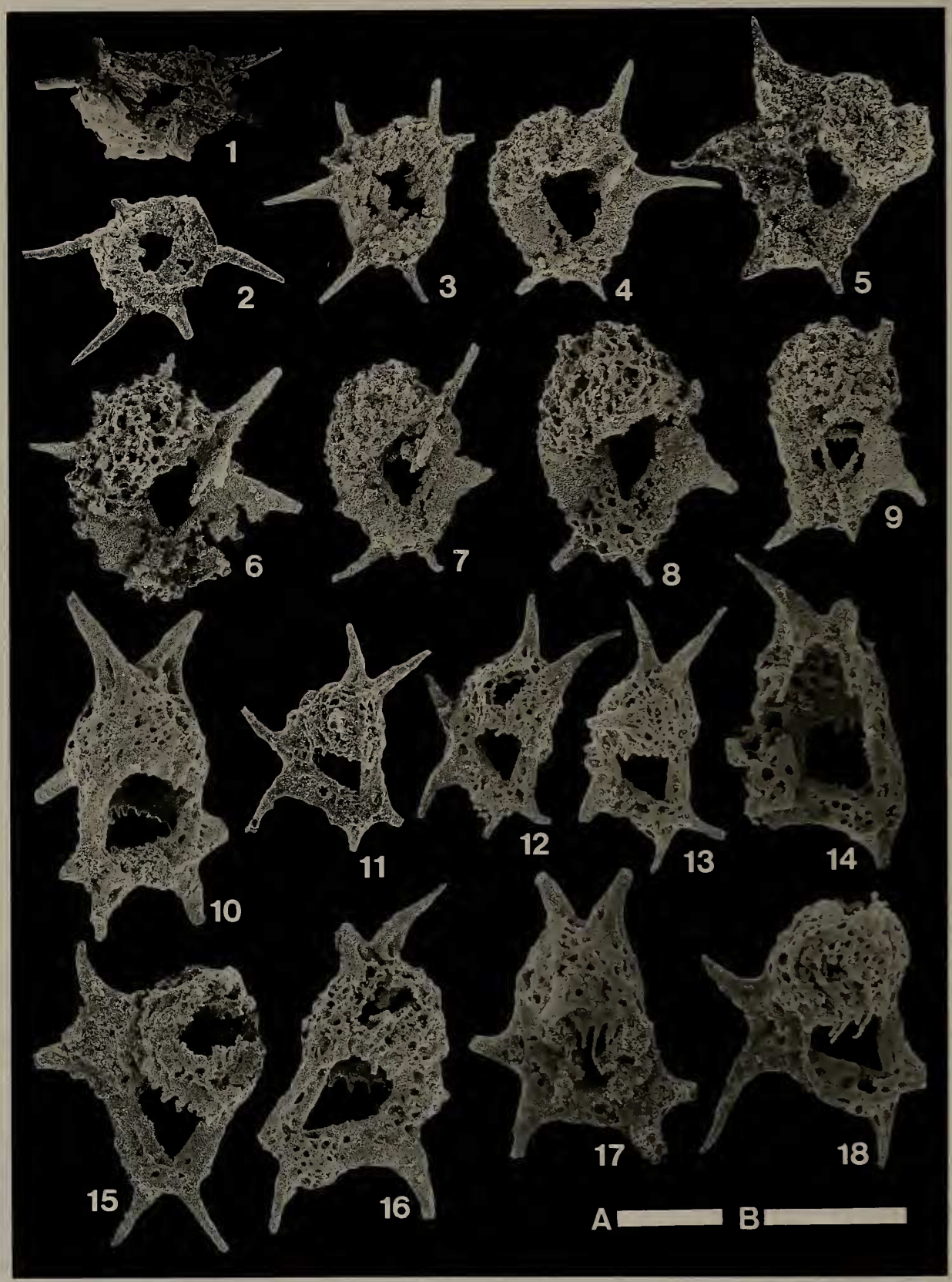
Glanta fragilis Wakamatsu, Sugiyama and Furutani, 1990

Figures 5-6—8

Glanta fragilis Wakamatsu, Sugiyama and Furutani, 1990, p. 180-181, pl. 12 ; Furutani, 1996, fig. 7-10, 11 ; Furutani, 1997, pl. 1, fig. 11.

Glanta sp. A Furutani, 1996, p. 76, fig. 7-8, 9.

Description.—Shell is suboval in anterior view and subtrapezoidal in lateral view. Subcircular basal aperture of the ventral portion of the shell faces a subtriangular to suboval central opening. A.t. and the dorsal part of i.t. are covered with the shell. A.a. is long, flat and tapered distally. B.d. is longer and thicker than i.d.. B.t. and i.t. rim the interior side of the lamellar patagium which is well-developed, wide and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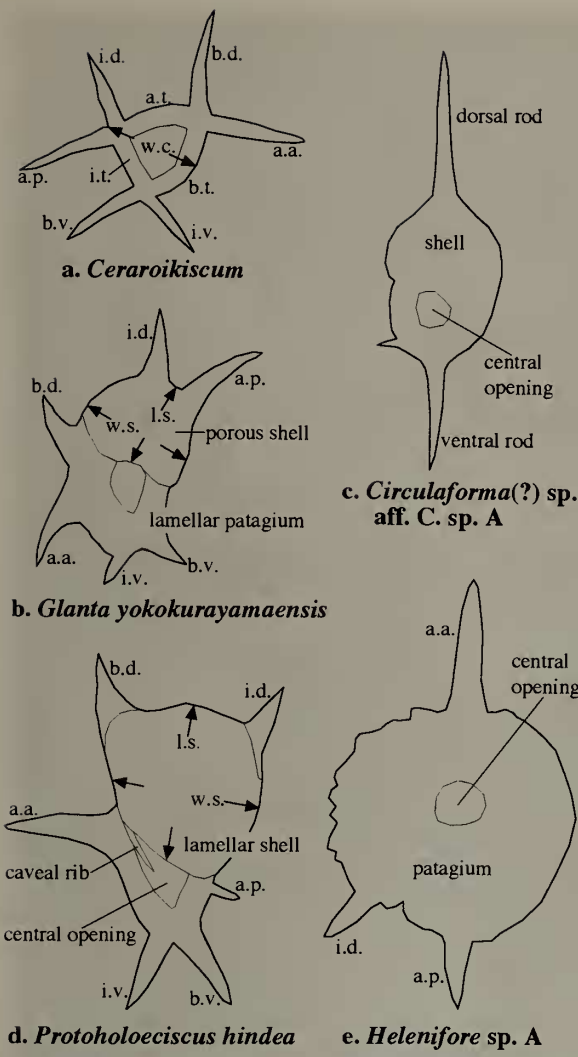


Figure 6. Terminology of skeletal structures of Devonian Ceratoikiscidae. a.a. : a-rod, anterior portion, a.p. : a-rod, posterior portion, a.t. : a-rod, triangle-forming portion, b.d. : b-rod, dorsal portion, b.v. : b-rod, ventral portion, b.t. : b-rod, triangle-forming portion, i.d. : i-rod, dorsal portion, i.v. : i-rod, ventral portion, i.t. : i-rod, triangle-forming portion, l.s. : length of shell, w.s. : width of shell.

flat. The junction of b- and i-rods is ornamented with patagial tissue. Pores on the shell and patagial tissue are circular to oval in shape and variable in size. A pair of caveal ribs extends from the junction of a- and b rods.

Material.—26 specimens from 2F to 3A of Section A and from 37C to 37E in Section B.

Range and occurrence.—Possible Emsian to Eifelian age. Nakahata Formation in the Yokokurayama Group.

Glanta sp.

Figures 5-9

Description.—Porous shell develops at the dorsal side of a. t.. The shell is suboval in anterior view and trapezoidal to suboval in lateral view. B.d. and i.d. connect with the shell and are enveloped in the lateral margin of the shell. The junction of b- and i-rods is ornamented with patagial tissue. Pores on the shell and the patagial tissue are circular to subcircular in shape and variable in size. A.t., b.t. and i.t. form an equilateral triangle in the central opening. Basal aperture faces to the central opening. The lamellar patagium is well developed and flat. A.a. is sturdy, rather flat and long. B.v. and i.v. are short and rather conical. B. d. is longer and thicker than i.d.. Caveal ribs remain uncertain.

Material.—Two specimens from 37C in Section B.

Remarks.—This species is similar to *G. fragilis* Wakamatsu, Sugiyama and Furutani in having porous shell, but it differs by having a.t. in the central opening.

Range and occurrence.—Possible Emsian to Eifelian age. Nakahata Formation in the Yokokurayama Group.

Glanta yokokurayamaensis sp. nov.

Figures 5-10—18

Diagnosis.—Porous shell covers a.t. and dorsal part of i.t.. l.d., a.p. and a pair of spines extending from the shell are robust and their bases are bladed.

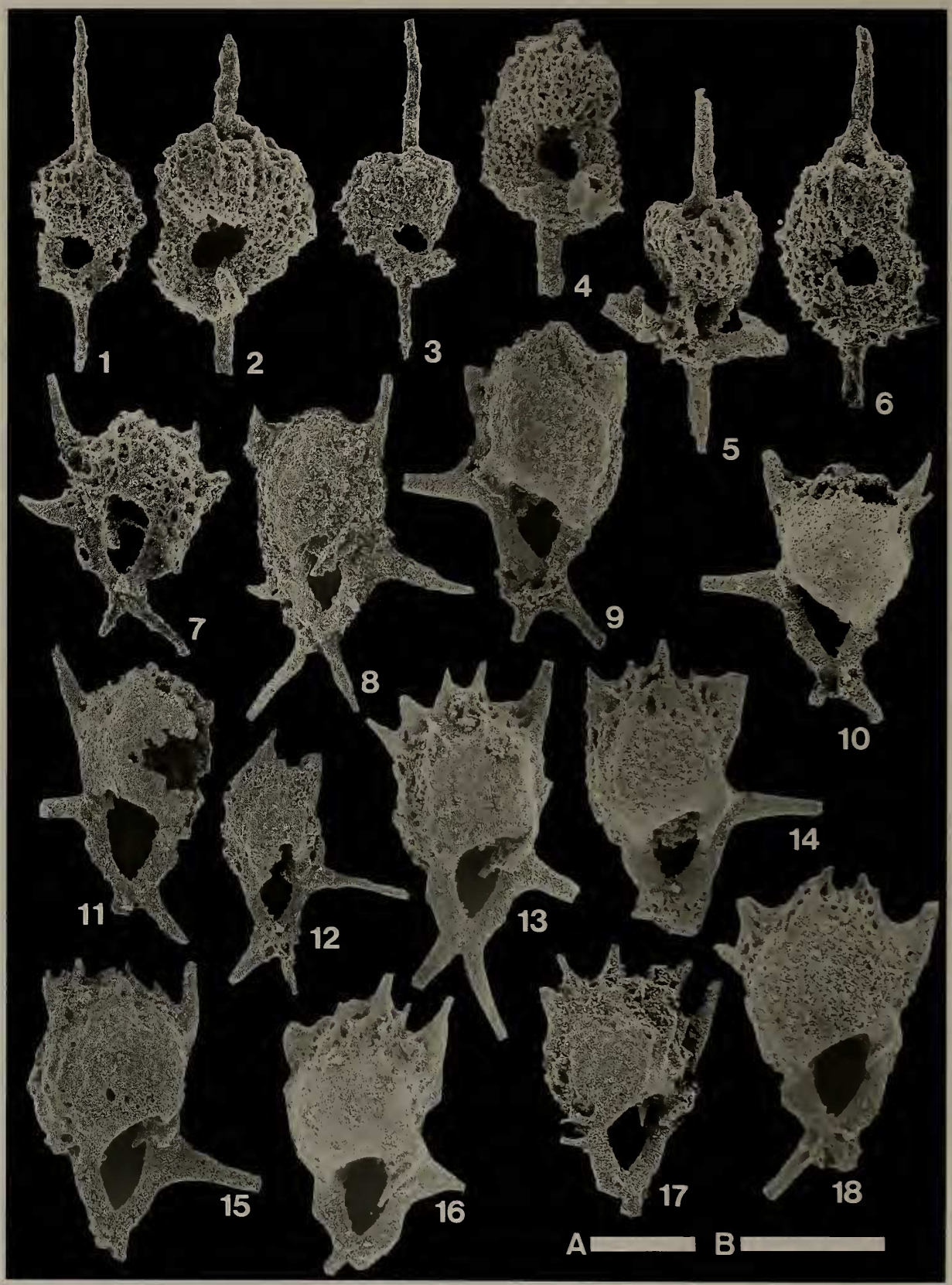
Description.—Shell is oval in anterior view and trapezoidal form in lateral view. The ventral margin of the shell is serrated. Several pairs of caveal ribs are traceable along the surface of the shell. Pores on the shell are circular to subcircular in form and irregular in size. Subcircular basal aperture faces central opening. B.t. and i.t. connect with the interior sides of lamellar patagium. The lamellar patagium with several pores is well developed and flat. Patagial tissue is often developed around the junction of b- and i-rods. Extratriangular rods are sturdy. A pair of spines, extending from the central part of the shell bilaterally symmetrically in an almost vertical plane, is thick and long. The spines and the extratriangular rods are tapered distally. l.d., a.p. and the spines are bladed at the base.

Measurements.—Measured features are shown in Figure 6-b.

Length of shell : 65-88, average 74, based on 25 specimens, in μm.

Width of shell : 85-100, average 92.

Figure 5. **1-3.** *Ceratoikiscum lyratum* Ishiga, 1 : OCU PR 0134, 3N, 2 : OCU PR 0135, 15E, 3 : OCU PR 0136, 37C. **4, 5.** *Ceratoikiscum turgidum* sp. nov., 4 : OCU PR 0137, 37C, holotype, 5 : OCU PR 0138, 15E. **6-8.** *Glanta fragilis* Wakamatsu, Furutani and Sugiyama, 6 : OCU PR 0139, 2J, 7 : OCU PR 0140, 37C, 8 : OCU PR 0141, 3A. **9.** *Glanta* sp., OCU PR 0142, 37C. **10-18.** *Glanta yokokurayamaensis* sp. nov., 10 : OCU PR 0143, 15C, holotype, 11 : OCU PR 0144, 15E, 12-18 : OCU PR 0145-51, 15C. Scale bar is 100 μm, A : 1-3, 11-13, B : 4-10, 14-18.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Material.—27 specimens from 15C, 15E and 15F in Section C.

Comparison.—This species differs from other species of *Glanta* in having robust and bladed i.d., a.p. and spines extending from the shell.

Range and occurrence.—Possible Eifelian age. Nakahata Formation of the Yokokurayama Group.

Etymology.—From the name of Mt. Yokokurayama, the study area.

Type specimen.—Holotype OCU PR 0143 (Figure 5-10) from 15C.

Genus ***Circulaforma*** Cheng, 1986

Circulaforma sp. aff. ***C.*** sp. **A** Stratford and Aitchison, 1997

Figures 7-1—6

Description.—Specimens possess elongate ring-like shell with three rods. The dorsal portion of the shell is large and oval in posterior and lateral view. Subcircular basal aperture faces to oval central opening. Pores on the shell are circular to subcircular in shape and irregular in size. The internal structure of the shell is not observed. Ventral and dorsal rods are prominent, opposite, long, sturdy, mostly straight and blunt at end. The ventral rod is longer than the dorsal rod. The third subsidiary rod is thin, delicate and short. All rods are circular in cross section. A pair of spines extends from the junction of the shell and basal rod bilaterally symmetrically in an almost vertical plane.

Measurements.—Measured features are shown in Figure 6-c.

Axial diameter of shell : 115-160, average 136, based on 10 specimens, in μm.

Axial diameter of central opening : 25-35, average 30.

Length of dorsal rod : 115-140, average 127.

Length of ventral rod : 60-80, average 72.

Material.—Ten specimens from 15C, 15E and 15F in Section C.

Comparison.—This form is similar to *Circulaforma* sp. A Stratford and Aitchison in having two opposite long rods and a ring-like fabric, but differs in the presence of developed shell at the dorsal portion. The assignment of this species to the genus *Ceratoikiscum* is difficult.

Range and occurrence.—Possible Eifelian age. Nakahata Formation in the Yokokurayama Group.

Genus ***Protoholoeciscus*** Aitchison, 1993

Description.—Triangular skeletal framework with bilaterally symmetric lamellar shell which is located between b.d. and i.d..

Comparison.—The disposition of rods of *Protoholoeciscus* is similar to that of *Glanta*, but it is distinguished by the presence of a lamellar shell. It differs from *Holoeciscus* in having a rather equilateral triangular framework (Aitchison, 1993).

Protoholoeciscus sp.

Figure 7-7

Description.—Small lamellar shell is clothed with a delicate and thin perforate sheet. Pores on the spongy layer are circular to subcircular in shape and irregular in size. Subcircular basal aperture faces a subtriangular to suboval central opening. Patagial tissue is weakly developed around the junction of b- and i-rods. A.t. is covered with the shell. B.d. is longer and thicker than i.d.. A.a. and b.d. are robust. A.p. and i.d. are short and delicate. All rods are circular in cross section. Caveal ribs remain uncertain.

Material.—One specimens from 37E in Section B and two specimens from 15E in Section C.

Remarks.—This species differs from other species of *Protoholoeciscus* in having a small shell with a perforate sheet which is regarded as the primitive feature of *Protoholoeciscus* as discussed later.

Range and occurrence.—Possible Emsian to Eifelian age. Nakahata Formation in the Yokokurayama Group.

Protoholoeciscus hindea Aitchison, 1993

Figures 7-8—12

Albaillellaria gen. indet. sp. Aitchison, Flood and Spiller, 1992, fig. 6, O-S.

Protoholoeciscus hindea Aitchison, 1993, p. 362, pl. 1, fig. 3 ; Stratford and Aitchison, 1997, pl. IV, A-B.

Glanta sp. B Furutani, 1996, p. 76, fig. 7, 12-13.

Glanta sp. Furutani, 1997, pl. 1, fig. 12.

Description.—Large lamellar shell is rectangular to trapezoidal in lateral view. A.a., b.d., b.v. and i.v. are robust. A.p. and i.d. are short and delicate. All rods are circular in cross section. Patagial tissue weakly developed around the junction of b- and i-rods. A pair of caveal ribs extends from the junction of a- and b rods. Subcircular basal aperture faces subtriangular to suboval central opening.

Material.—44 specimens from 3B to 3N in Section A and 37E in Section B.

Range and occurrence.—Possible Eifelian age. Nakahata Formation in the Yokokurayama Group ; Gamilaroi Terrane (Stratford and Aitchison, 1997) and Djungati Terrane (Aitchison *et al*., 1992 ; Aitchison, 1993), N.S.W., Australia.

Figure 7. 1-6. *Circulaforma* sp. aff. *C.* sp. A Stratford and Aitchison, 1 : OCU PR 0152, 15E, 2 : OCU PR 0153, 15E, 3 : OCU PR 0154, 15F, 4, 5 : OCU PR 0155-156, 15C, 6 : OCU PR 0157, 15E. **7.** *Protoholoeciscus* sp., OCU PR 0158, 15E. **8-12.** *Protoholoeciscus hindea* Aitchison, 8 : OCU PR 0159, 3N, 9 : OCU PR 0160, 3B, 10 : OCU PR 0161, 3I, 11, 12 : OCU PR 0162-163, 3L. **13-18.** *Protoholoeciscus spinosus* sp. nov., 13 : OCU PR 0164, 3B, holotype, 14 : OCU PR 0165, 3N, 15-17 : OCU PR 0166-168, 3B, 18 : OCU PR 0169, 3B. Scale bar is 100 μm, A : 1, 3, 12, B : 2, 4-11, 13-18.

Protoholoeciscus spinosus sp. nov.

Figures 7-13—18

Diagnosis.—Several projections extend from the dorsal part of a large lamellar shell.

Description.—Large lamellar shell is trapezoidal to rectangular in lateral view and oval in anterior view. The internal structure of the shell is not observed. Several irregularly arranged pores on the shell are circular to subcircular. Several projections are short, delicate, tapered distally, arise from the dorsal part of the shell and trend in a dorsal direction. A.a., b.d., b.v. and i.v. are long and robust. A pair of caveal ribs extends from the junction of a- and b rods. All rods, caveal ribs and projections are circular in cross section. Patagial tissue is often ornamented around the junction of b- and i-rods. Subcircular basal aperture faces the central opening, which is subtriangular to suboval.

Measurements.—Measured features are shown in Figure 6-d.

Length of shell : 70-105, average 90, based on 15 specimens, in μm.

Width of shell : 75-105, average 91.

Material.—15 specimens from 3B, 3C and 3I to 3N in Section A.

Comparison.—This species is distinguished from other species of *Protoholoeciscus* in possessing several projections from the dorsal part of the shell.

Range and occurrence.—Possible Eifelian age. Nakahata Formation of the Yokokurayama Group.

Etymology.—This name is derived from the Latin adjective *spinosus*, meaning thorny.

Type specimens.—Holotype OCU PR 0164 (Figure 7-13); Paratype OCU PR 0165 (Figure 7-14). Both from 3B.

Protoholoeciscus ochiensis sp. nov.

Figures 8-1—6

Diagnosis.—This species is characterized by an equilateral triangular shape with long b.d. and slender b.v. and i.v.. All rods are circular in cross section.

Description.—Large lamellar shell is subtrapezoidal in lateral view. Pores on the shell are circular to subcircular. A. a. is weakly developed and a.p. is absent. A.t. remains uncertain. B.d. is longer and thicker than i.d.. B.v. and i.v. are thin and slender. Patagial tissue is weakly developed around the junction of b- and i-rods. A pair of spines is short, delicate and extends bilaterally symmetrically from the junction in the vertical plane. A pair of caveal ribs extends from the junction of a- and b rods. Ovate basal aperture faces central opening, which is subtriangular to oval.

Measurements.—Measured features are shown in Figure 6-d.

Length of shell : 70-115, average 97, based on 19 specimens, in μm.

Width of shell : 95-135, average 115.

Material.—19 specimens from 15C, 15E and 15F in Section C.

Comparison.—This species differs from *Protoholoeciscus hindea* Aitchison and *Pr. spinosus* sp. nov. in having an equilateral triangular shape with slender b.v. and i.v. This species is distinguished from *Pr. triangularis* (Wakamatsu, Sugiyama and Furutani) in having rod-like b.d.

Range and occurrence.—Possible Eifelian age. Nakahata Formation of the Yokokurayama Group.

Etymology.—From the town of Ochi, where the study area is situated.

Type specimen.—Holotype OCU PR 0170 (Figure 8-1) from 15F.

Protoholoeciscus triangularis (Wakamatsu, Sugiyama and Furutani, 1990)

Figures 8-7—9

Glanta triangularis Wakamatsu, Sugiyama and Furutani, 1990, p. 182, pl. 13, figs. 1-7 ; Furutani, 1996, fig. 7, 15.

Description.—Large lamellar shell is subtrapezoidal in lateral view. A.a., b.d., b.v. and i.v. are robust. B.d. is thickest and deeply grooved. Patagial tissue is weakly ornamented around the junction of b- and i-rods. A pair of spines extends bilaterally symmetrically from the junction in the vertical plane. A pair of caveal ribs extends from the junction of a- and b rods. Pores on lamellar shell are circular to subcircular. Subcircular basal aperture faces subtriangular to ovate central opening.

Material.—Eight specimens from 15C, 15E and 15F in Section C.

Remarks.—Although this species was assigned to genus *Glanta* in previous work (Wakamatsu *et al*., 1990), it belongs to *Protoholoeciscus* based on the presence of a lameller shell (Stratford and Aitchison, 1997). This species differs from other species of *Protoholoeciscus* in having deeply grooved b.d..

Range and occurrence.—Possible Eifelian age. Nakahata Formation of the Yokokurayama Group.

Genus ***Helenifore*** Nazarov and Ormiston, 1983

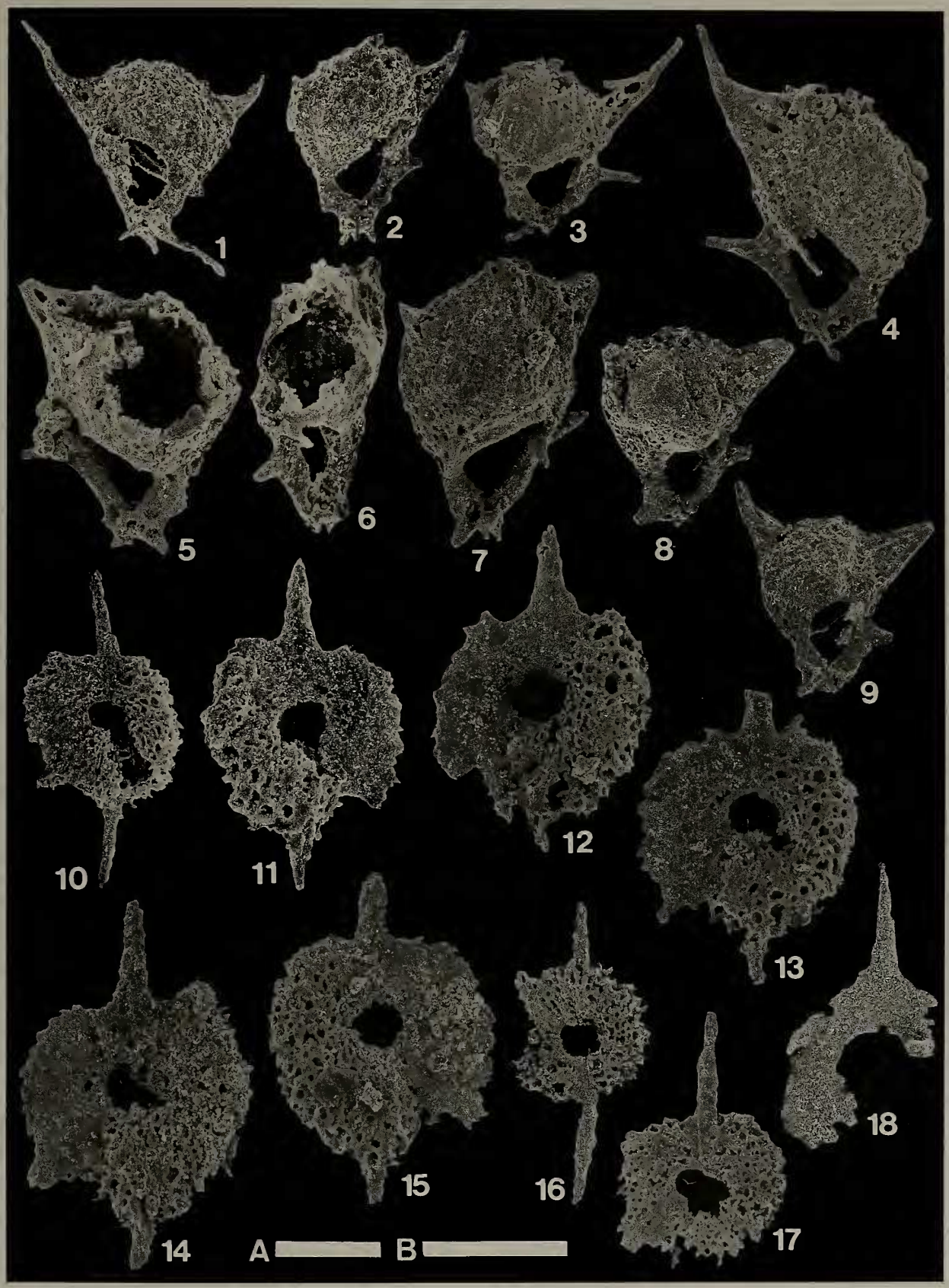
Helenifore sp. **A** Stratford and Aitchison, 1997

Figures 8-10—17

Helenifore sp. Aitchison, Flood and Spiller, 1992, fig. 6C.
Helenifore sp. A Stratford and Aitchison, 1997, pl. III, A-D.

Description.—This species is characterized by large disk-

Figure 8. 1-6. *Protoholoeciscus ochiensis* sp. nov., 1 : OCU PR 0170, 15E, holotype, 2 : OCU PR 0171, 15E, 3-5 : OCU PR 0172-174, 15C, 6 : OCU PR 0175, 15E. **7-9.** *Protoholoeciscus triangularis* (Wakamatsu, Sugiyama and Furutani, 1990), OCU PR 0176-178, 15C. **10-17.** *Helenifore* sp. A Stratford and Aitchison, 10 : OCU PR 0179, 15F, 11 : OCU PR 0180, 15E, 12-16 : OCU PR 0181-185, 15C, 17 : OCU PR 0186, 15E. **18.** *Helenifore* sp. B, OCU PR 0186, 37C. Scale bar is 100 μm, A : 1-3, 8-10, 16-18, B : 4-7, 11-15.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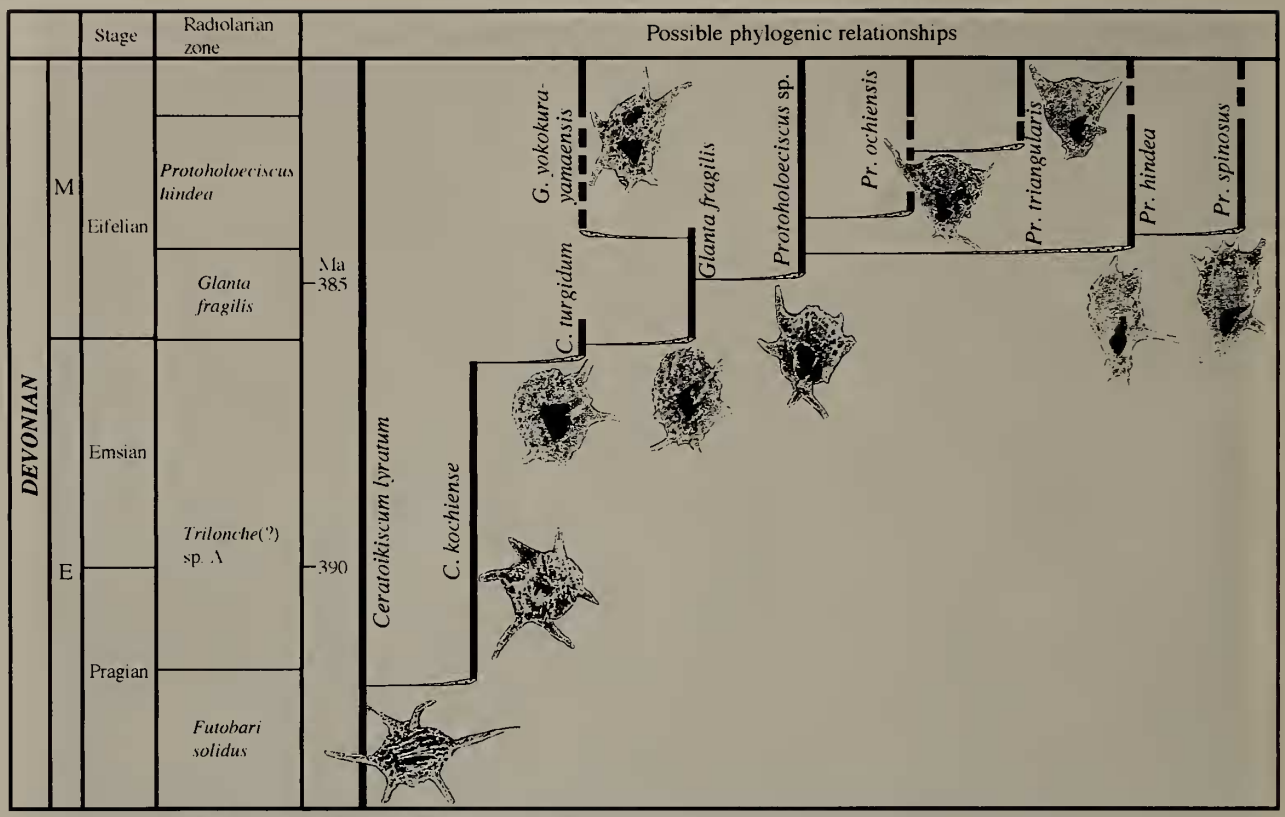

Figure 9. Possible phylogenetic relationships among *Ceratoikiscum, Glanta* and *Protoholoeciscus*.

like shape with two prominent rods which extend in opposite directions in the horizontal plane (Figure 6-e). Developed patagium is porous, large, extensive and circular to subcircular. Pores on the patagium are circular to oval in shape and irregular in size. Central opening is circular to oval. Opposite a.a. and a.p. are sturdy, acute, slightly curved, blunt at end and variable in length. l.d. is rather short. All rods are circular in cross section.

Material.—33 specimens from 3I, 3L and 3N in Section A and 15C, 15E and 15F in Section C.

Comparison.—This species is distinguished from *Helenifore planus* Umeda (1997) in having a large patagium and rather short rods and in absence of b.d. and b.v..

Remarks.—Stratford and Aitchison (1997) described the *Helenifore* sp. A Assemblage from eastern Australia and assumed the age to be Eifelian.

Range and occurrence.—Possible Emsian to Eifelian age. Djungati Terrane (Aitchison et *al*., 1992) and Gamilaroi Terrane (Stratford and Aitchison, 1997) in the New England Fold Belt, eastern Australia; Nakahata Formation of the Yokokurayama Group.

Discussion

Five genera and twelve species of Ceratoikiscidae from three sections are described in this paper. *Ceratoikiscum* and *Helenifore* are known from the Silurian to Carboniferous, whereas *Glanta* and *Protoholoeciscus* are restricted to the Devonian. Furutani (1996) examined the evolution of Devonian Ceratoikiscidae based on materials from the Nakahata Formation and recognized morphologic similarities in well-developed patagium between *Ceratoikiscum* and *Glanta*. Emsian (late Early Devonian) species of *Ceratoikiscum* (*C. kochiense* Umeda) from the Konomori area in the Kurosegawa Terrane possesses developed lamellar patagium and robust rods (Umeda, 1997). This species seems to have arisen from *C. lyratum* Ishiga with the addition of developed patagium (Umeda, 1997). *C. kochiense* is similar to *C.* sp. in this paper and *Glanta fragilis* Wakamatsu, Sugiyama and Furutani in having developed lamellar patagium, rather sturdy a.a. and short and rather conical b.v. and i.v. The shape of the inflated swell of *C.* sp. is similar to the porous shell of *G. fragilis*. Accordingly *G. fragilis* seems to have arisen from *C.* sp. which seems in turn to have evolved from *C. kochiense*. *G. fragilis* appears to be the primitive form among *Glanta* species and gave rise to *G. yokokurayamaensis* sp. nov. The perforate shell of *Glanta* changed to a lamellar shell in successive stratigraphic sections (Furutani, 1996). *Glanta* morphologically resembles *Protoholoeciscus* in its framework. The perforate sheet on small lamellar shell of *Protoholoeciscus* sp. in this paper is similar to the porous shell of *Glanta*; this feature is regarded as transitional between *Glanta* and *Protoholoeciscus*. *Pr.* sp. seems to have evolved from *G. fragilis* with the change of

shell from porous to lamellar type. *Pr.* sp. is similar to *Pr.* ochiensis sp. nov. in having an equilateral triangular framework and subtrapezoidal shell. *Pr.* sp. gave rise to *Pr. ochiensis* and *Pr. hindea* Aitchison, in which the perforate sheet on the shell is lost. *Pr. triangularis* (Wakamatsu, Sugiyama and Furutani) possesses an equilateral triangular framework with bladed rods. *Pr. triangularis* seems to have arisen from *Pr. ochiensis* with the change of rods from circular to bladed in cross section. *Pr. hindea* and *Pr. spinosus* sp. nov. possess a large trapezoidal to rectangular shell. *Pr. spinosus* seems to have arisen from *Pr. hindea*.

Aitchison (1993) considered that *Protoholoeciscus* is the transitional form between *Ceratoikiscum* and *Holoeciscus*. Based on the above-mentioned morphologies and biostratigraphic distributions, it is supposed that *Protoholoeciscus* evolved from *Ceratoikiscum* via *Glanta* (Figure 9). *Protoholoeciscus* is regarded as the ancestor of *Holoeciscus*. Acquisitions of shell of Ceratoikiscidae show drastic and significant evolutionary change in short time, namely Emsian to Eifelian age.

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